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A Functional-Structural Plant Model--Theory and Applications in Agronomy‡

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Abstract: Functional-structural plant models (FSPM) simulate plant development and growth, usually accompanied with visualization of the plant 3D architecture. GreenLab is a generic and mechanistic FSPM: various botanical architectures can be produced by its organogenesis model, and the plant growth is governed by the competition on biomass among growing organs. A distinguished feature of GreenLab model is that, its organogenesis (in terms of the number of organs) and growth (in terms of organ biomass) are formulated with recurrent equations. It facilitates analytical study of model behaviour, bug-proof of simulation software, and application of efficient optimization algorithm for parameter identification or optimal control problems.

Currently several levels of GreenLab model exist: (1) the deterministic one (GL1): plants have a fixed pattern for development without feedback from the plant growth; (2) the stochastic level (GL2): pant organogenesis parameters are probabilistic; (3) the feedback model (GL3): the plant development is dependent on the dynamic relationship between biomass demand and supply (and in turn the environment). It makes it possible to deal with different kinds of behaviour observed in real plants.

This paper presents recent typical GreenLab applications: (1) calibration of GL1 for getting sink and source functions of maize; (2) fitting of GL2 on organogenesis of wheat plant; (3) rebuilt of the rhythmic pattern of cucumber using GL3; (4) optimization of model parameters to improve yield, such as leaf (for tea) or wood quantity (for trees); (5) the possible introduction of genetic information in the model through detection of quantitative trait loci for the model parameters; (6) simulation of plant competition for light.

Keywords: GreenLab, FSPM, GL1, GL2, GL3, plant optimization, QTL, plant competition

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1 Introduction

In past years, Functional-Structural Plant Models (FSPMs) were attracting interest from plant modellers (Vos et al 2007). GreenLab methodology, began to develop near ten years ago, have been applied for many different crops, including maize (Guo et al 2006, Ma et al 2007, Ma et al 2008), tomato (Dong et al 2008), chrysanthemum (Kang et al 2006), pine tree (Guo et al 2007), Arabidopsis (Letort et al 2007), wheat (Kang et al 2008). Other undergoing GreenLab-based application for various purposes includes modelling on beech tree, rice, cotton, cucumber, sweet pepper, etc. On the other hand, theoretical work on GreenLab kept on undergoing in parallel: the formalism of the topological model (de Reffye et al 2003), structure factorization of complex plant structure for fast computation (Cournède et al 2006), analytical computation of mean and variance of stochastic model (Kang et al 2007), generation of rhythmic pattern of branch or fruits from GreenLab dynamic system (Mathieu et al 2007), link between GreenLab parameters and QTL (Letort et al 2008), computation of inter-plant competition (Cournède et al 2008). Software based on GreenLab model has been developed for plant simulation and model calibration, including CornerFit, GreenScilab, and DigiPlante.

In this paper, we review the general form of GreenLab model, present its different levels, and one of its application on real plants. Three theoretical works are presented to show future possible application with GreenLab.

2 General presentation

A time step (a growth cycle, GC) in GreenLab model corresponds to the temperature sum it takes to generate a growth unit (GU), being a metamer for crops or an annual axis for trees. The plant development is simulated with automaton (Zhao et al 2001). All organs (leaf blade and petiole, internode pith and layer, female and male organs, root system) are sinks that share biomass from a common pool. The sink strength of an organ varies with time, described by an empirical function. As a result of competition, the weight of each organ is computed, as well as the size of organs. Beside the seed that provide biomass in initial GCs, leaf is the main source organ. The production of a plant is a function of green leaf area.

The number of GC since the appearance of an organ or a branch is called chronological age (CA). Another feature is physiological age (PA). PA is expressed in integer values too, being one for main stem. Branches are generally physiologically older than its parent axis, except the case of reiteration. The maximum PA in plant is noted as P_m. Organs of the same CA and PA are supposed to have the same sink strength and thus the same weight (except for internodes that can have secondary growth). Based on the notion PA, using substructure decomposition (Cournède et al

2006), the number of organs in each GC can be computed with equations without resorting to simulation.

A highly compact form of GreenLab model can be expressed as in Eqn. 1:

$$\begin{aligned} \mathbf{N_O} &= f(\mathbf{P_d}, \mathbf{Q}, T) \\ \mathbf{Q} &= f(\mathbf{N_O}, \mathbf{P_g}, E) \end{aligned} \tag{1}$$

In Eqn. 1, $\mathbf{N_o}$ are the number of organs of each CA and PA in plant structure at each growth cycle, O=B (blade), S (sheath), pith (P), layer (L), female (F), male (M), or root (R). $\mathbf{P_d}$ are the development parameters that define the plant topology, including the number and PA of leaves, buds, flowers and axillary buds in each kind of GU, repetition time of GU in an axis before mutate into another PA, etc. T is the air temperature. The development speed of the plant, or number of days per GC, is mainly decided by the air temperature.

Q can be any quantity of the biomass of plant at each growth cycle: weight of individual organs, or total weight of a kind of organ (say fruits), or weight of full plant. E is the environmental data. $\mathbf{P_g}$ is the growth parameters that effect the biomass production and partitioning among organs. $\mathbf{P_g}$ includes:

(1) the relative sink strength of organs ($P_O{}^p$), p being PA of organs. That of blade in main stem is set to one as the reference, i.e. $P_O{}^p=1$;

(2) parameters of sink variation function ($\varphi_O{}^i$) that describe the change of sink strength of individual organs, i being CA of organs. The actual sink strength of an organ of PA p and CA i is thus $P_O{}^p \varphi_O{}^i$;

(3) the empirical parameters of source function (see Eqn. 3);

(4) functioning time (t_f), expansion time (t_x) of organs;

(5) internode allometric parameters and specific leaf weight (e).

The total demand for biomass of plant is computed as the sum of sink strength of all growing organs, as in Eqn. 2:

$$D_n = \sum_O \sum_{p=1}^{P_m} \sum_{i=1}^{tx_o} N_O{}^{p,i} P_O \varphi_O^i \tag{2}$$

A commonly used biomass production function of GreenLab is inspired by the Beer-Lambert law of light extinction:

$$Q_n = E_n \beta (1 - \exp(-\gamma S_n)) \tag{3}$$

Where β, γ are empirical model parameters estimated by model inversion, S_n is the total green leaf area of the plant at growth cycle n.

The biomass allocation to an organ is then

$$\Delta q_n{}^{p,i} = P_O \varphi_O^i \frac{Q_{n-1}}{D_n} \tag{4}$$

The biomass of an organ is sum of increment since its appearance:

$$q_n^{p,i} = \sum_{j=1}^{i} \Delta q_{n-j+1}^{p,j} = \sum_{j=1}^{i} P_O \varphi_O^j \frac{Q_{n-j}}{D_{n-j+1}} \quad (5)$$

From Eqn. 5, it can be seen that the biomass of an organ depends on the ratio (Q/D) during its life span. Although organs of the same type and PA have the same sink strength, their final biomasses differ if they appear at different moments.

3 Versions of the GreenLab model and their applications

Different levels of GreenLab model have been developed and applied, namely GL1, GL2, and GL3. In order that the model behave closely to the real plant, it is necessary to get a set of suitable parameters (model calibration). Part of them can be observed directly, such as specific leaf weight, internode allometric parameter, development parameters (case of deterministic model), functioning and expansion time of organs. Organ sink strength, sink expansion functions, and empirical parameters for biomass production, are difficult to measure directly. These (hidden) parameters are estimated using non-linear least square method aiming at minimizing the model output and measured data. Besides these common parts, different levels of model have their specific parameters, see below.

3.1 GL1 and case study on maize

GL1, the basic version, has been applied to simulate many plants: maize (Ma et al 2007), pine tree (Guo et al 2006), arbidobisis (Letort et al 2008), chrysanthemum (Kang et al 2006), etc. In GL1, the plant development (and consequently the number of organs) is not influenced by the biomass supply, but follows a fixed pattern. The form of GL1 is thus as in Eqn. 6.

$$\begin{aligned} \mathbf{N_O} &= f(\mathbf{P_d}, T) \\ \mathbf{Q} &= f(\mathbf{N_O}, \mathbf{P_g}, E) \end{aligned} \quad (6)$$

In the case that the plant is of single stem structure, the numbers of organs are easy to compute, and one can concentrate on sink-source parameter.

Growth rate Q_n is the increment in biomass in a growth cycle for the whole plant or each individual organ. For field plants, the growth rate Q_n, and organ growth rate $\Delta q_o(n)$ are internal and transient variables, and they are technically difficult to be directly measured. Therefore, the source and sink functions cannot be separately determined by using classical curve fitting methods. On the other hand, the plant architecture and organ biomass are accumulative results of the dynamical processes since the plant emergence, including plant growth and organ development. From the modeling point of view, since GreenLab model output variables (number, size and mass of organs) implicitly and nonlinearly depend on the hidden parameters in the recursive simulation process, thus these

parameters can be identified through inverse modeling, i.e., the parameter values are determined by minimizing the differences between observed and simulated variables. When this is achieved, GreenLab model can fit best to plant morphological and architectural data observed at several points of time. There are several optimization algorithms available to minimize the proposed objective function, for example, the Levenberg-Marquardt method, genetic algorithms, or stochastic methods. The Levenberg-Marquardt method is practically proved more efficient than the others in terms of computation time.

We illustrate how GL1 is calibrated on the maize plant as an example. Under normal condition of moderate density, the final structure of maize plant is made up of four types of organs: the main stem, the leaf sheathes and blades, a tassel (the male organ) at top, and one or several ears (the female organs) set at different nodal positions along the stalk. For maize, the variation of sink strength of individual organs was taken as the form of Eqn. 7:

$$\begin{aligned} &\varphi_O(j) = \begin{cases} g_O(j)/\mu_O & 1 \le j \le tx_O \\ 0 & j > tx_O \end{cases}, \\ &where\ g_O(j) = \left(\frac{j-0.5}{t_O}\right)^{\alpha_O - 1}\left(1-\frac{j-0.5}{t_O}\right)^{\beta_O - 1}, \\ &\mu_O = \max\{g_O(j) \mid 1 \le j \le tx_O\}, O = B, S, I, F, M \end{aligned} \tag{7}$$

There are 12 parameters to be estimated for maize plants, including two empirical parameters of the source function (β and γ in Eqn. 3), and ten parameters of the sink functions (P_O in Eqn. 2 and α_O in Eqn. 7, O = B, S, I, F, M, denoting leaf blade, sheath, internode, ear and tassel, respectively, $\alpha_O + \beta_O \equiv 5$ for all organs).

During the course of plant development and growth, plants were regularly sampled and detailed measured, including size (length, diameter, area) and fresh or dry mass of each organ. The data were stored in a specified structure according to the position, type and attribute of organs. From these data the target can be constructed for the model to fit. In order to get an estimate of the source and sink parameters, we use the weighted least-square criterion:

$$\phi(\boldsymbol{\theta}) = (\mathbf{Z} - F(\boldsymbol{\theta}))^T \mathbf{W} (\mathbf{Z} - F(\boldsymbol{\theta})) \tag{8}$$

where $\mathbf{Z}$ is the target vector consists of measurement data on plant samples at several stages; $\boldsymbol{\theta}$ is the parameter vector to be estimated, a subset of $\mathbf{P_g}$; $F(\boldsymbol{\theta})$ is a vector function (i.e., the recursive simulation equations) with respect to $\boldsymbol{\theta}$, whose components are simulated data corresponding to $\mathbf{Z}$; $\mathbf{W}$ is a diagonal positive matrix which weights the various observations.

GL1 model where fitted to three stages of maize plants. The fitting results are shown in Fig. 1. Based on the calibrated parameters, the model was tested against independent data from different years (Ma et al 2007) and different population densities (Ma et al 2008).

3.2 GL2 and case study on wheat

GL2 is a stochastic model, having the same form as Eqn. 6, whereas $\mathbf{P_d}$ are stochastic variables. It takes into account the variations in topology among plants caused by bud activities, such as bud dormancy and bud death. Accordingly, the number of organs, $\mathbf{N_O}$, are stochastic variables. Their mean and variance, necessary for computing those of biomass, can be computed analytically aside Monte-Carlo simulations (Kang et al 2007). At a result, the effect of plant topology (dense or sparse) on plant production GL2 can be shown immediately. GL2 is interesting for plants show strong randomness in topology, for example, wheat plant. Using tiller bud outgrowth probability and tiller survival probability, the number of phytomers in tillers and the final remaining tillers were well simulated, as shown in Fig. 2. The second step of model calibration concerns fitting on biomass production. This procedure is similar to GL1 except that the numbers of organs, $\mathbf{N_O}$, are the mean values from plant samples. In other word, the average plant is fitted, representing the common plant among those of various topologies.

In more general sense, the growth parameter, $\mathbf{P_g}$, are also stochastic variables. It is meaningful for genetic application of the model. The biomass production is a complex nonlinear function of both categories of parameters. The analytical mean and variance of **Q** can be computed using differential statistics.

3 GL3 and sweet pepper

GL3 is a feedback version, having the same form as Eqn. 1 regarding the biomass production but the topological events of the plant are assumed to be controlled by the ratio of biomass (*Q*; Eqn. 3) to demand (D; Eqn. 2), that is to say that the numbers of the different type of organs $\mathbf{N_O}$ are computed as functions of this ratio. It allows reproducing the plant phenotypic plasticity as the number of organs depending on the plant vigour.

As an example, this GL3 model can be used to simulate the cyclic patterns of fruits that have been observed in the sweet pepper plant (Marcelis et al 2004) or in the cucumber plant (Marcelis, 1992). Fruit abortion can occur within the first days after fruit anthesis. In the GL3 model, we assume that if the ratio of biomass to demand is under a given threshold a few growth cycles after the fruit appearance, then the one will abort. Otherwise it will continue growing. This model was calibrated on pruned cucumber plants where the fruit growth is not limited by fruit initiation (Mathieu et al 2008). Fig. 3 shows the differences between the plant measurements and the model simulation. Fruits appeared on the plant when the ratio of biomass to demand exceeds a threshold (Fig. 4) which explains the two waves of fruits on the stem. The cyclic patterns of fruits are explained as a consequence of the assimilate competition between organs.

4 Theoretical study

The virtual plant itself as described by GreenLab model is a complex dynamic system. As it can behave close to real plants, it is meaningful to do virtual experiment on GreenLab plants. The theoretical studies present here are experiments done in computer. These works may pioneer the following work of applications.

4.1 Possible link with Quantitative Trait Loci (QTL)

In maize (Ma et al 2007) and tomato (Dong et al 2007), although the relative sink strength (of pith and fruit) vary, their expansion function remain the same for plants grown under different population densities. Consequently, it can be hypothesized that some of GreenLab parameters are species-specific and gene-based. Let Y denote the vector of these 'genetic' parameters. Introducing genetics in the model allows simulating plant reproduction and studying the evolution in time of a virtual population without requiring to time- and space- consuming experiments. In our model, the genotype of the plant is defined as a set of two vectors C_1 and C_2, representing the chromosomes (for sake of simplicity, only pairs of chromosomes are considered, although maize is generally haploid). The components of these vectors (alleles) are positive real numbers representing the parameter variation around a reference value Y_{ref}. An application f defines the rules of allele expression (dominance or additivity) and then the 'genetic' vector of GreenLab parameters Y is calculated as a product of matrices:

$$Y = C \times A \times f(C_1, C_2) \quad (9)$$

A is a matrix defining the influence of genes on each parameter, including pleiotropic rules (one gene has an influence on several parameters) or combinations of several gene effects on one parameter. C is a diagonal matrix introduced to ensure that the coefficients of Y are of the same order range (similar to barycentre calculation). Reproduction between two plants is simulated with realistic rules (Poisson law) driving the probability of crossing-over occurrences, see Letort et al. (2007) for details. It allows generating a virtual mapping population (recombinant inbred lines) to simulate the procedure of quantitative trait loci (QTL) detection, as done by geneticists on real plants (de Vienne 2003). Their goal is to localize the chromosomal segments (called QTL) that contain genes of interest (influencing the yield, for instance). In our model, QTL detection is analogous to determination of the coefficients of matrix A that drives the link between the plant genotype and the model parameters. Results shown in Fig. 5 are consistent with the opinion defended in several recent papers that underlined the potential benefits of introducing physiological knowledge into breeding programs (e.g. Chapman et al 2003; Hammer et al 2006; Tardieu et al 2003; Yin et al 2003). Our study illustrated that QTL detection on model parameters is more accurate on model parameters than on the classical morphological data such as cob weight (Fig. 5). We conclude that this method is worthy to be tested on real plant populations. GreenLab

parameters provide new criteria to renew the breeding process and to characterize model-based ideoptypes.

4.2 Yield optimization

As GreenLab is a mathematical model, it is possible to apply various optimization algorithms. Optimization on plants helps revealing the relationship between sources and sinks, and guiding us the direction in cultivation and genetic operation.

The optimization applications on GreenLab can be classified into two categories. If the parameters on which we optimize are related to genetic factors, such as sink variation of organs, their positions, etc, this kind of optimization problems belong to the classical multivariate optimization problem. If the variables to optimize are related to cultivation methods, such as water supply strategy (Wu et al 2005), pruning strategy, etc, this kind of problems belongs to optimal control problem. Here we present several optimization problems of different aims based on GreenLab model.

There are two basic optimization problems: optimization with or without constraints. Most optimization problems for plant growth can be classified to constrained ones. For example, in the domain of forestry, the volume (quantity) and quality of wood are of primary importance, from both economic and mechanic point of view. In GreenLab model, wood quantity is impacted by the sink strength for cambial growth and a coefficient that determines how biomass for cambial growth is allocated to each internode. Optimization on these two parameters gives the best yield of wood. On the other hand, wood quality is related to the geometrical shape of a bole and branches, which is controlled by mechanical parameters. Given the total biomass for cambial growth, if too much biomass is allocated to the branches, the biomass partitioned to the bold is not sufficient. Otherwise, if allocation is too much for the bole, the load of the bole will be too heavy and fall down easily, see Fig. 6. As a result, besides maximizing the bole weight, the angle of the bold at the top is limited under a threshold. The optimization problem on wood quantity and quality for a tree is the classical optimization problem with constraints. The preliminary results are to be published (accepted by IUFRO 2008).

Pruning is a common cultivation action in agriculture or forestry, in order to make plants growing better and to get better yield. For example, most of side branches of tomatoes are removed to make sure fruit yield. Obviously the behavior of plant is modified if pruning is done during plant growth. A special case is to prune leaves, such as tea plant. Here leaf plays double roles: it is not only the source organs the provide biomass to whole plant, but also the yield. For this problem, we add a control variable that represents the proportion of number of leaves pruned among the living leaves. With the objective being maximizing pruned leaves, it is an optimal control problem. This work is to be published soon. An ongoing optimization issue concerns the relationship among palm tree, insects and parasites. In this system, leaves produce biomass through photosynthesis, insects

eat leaves and parasites suppress the population growth of insects. The optimization problem is complex because of interaction among the three actors. It is necessary to study the population growth of insects and parasites, both affect significantly the growth behaviour of the palm tree. In addition, to avoid destroying leaves, pesticide is used. Considering the fact that pesticide kills not only insect adults but also parasite adults, and the price of pesticide is very expensive, in order to reduce the cost and increase its use efficiency (kill only insect adults), it is important to decide when pesticide is put to palm tree. This is also an optimal control problem.

4.3 Plant competition

GreenLab is an individual-based plant growth model. However, for applications in agriculture and forestry, it has to be extended to the scale of plant population. For this purpose, inter-plant competition for light is taken into account, see Cournède et al (2008).

For high density crops at full cover, the model should be equivalent to the classical equation of field crop production. For example, Howell and Musick (1985) showed that biomass production is proportional to crop transpiration *T*. It is driven by the potential evapotranspiration, the soil water content and the exposed green leaf surface area, evaluated using Beer-Lambert's extinction law. If at cycle *n*, E_n denotes the product of the potential evapotranspiration modulated by a function of the soil water content, *k* is the Beer-Lambert extinction coefficient related to leaf angular deviation and LAI_n is the leaf area index, T_n is estimated as:

$$T_n = E_n\left(1-\exp\left(-k\,LAI_n\right)\right) \tag{10}$$

Finally, the biomass production per unit surface area Q_n^c is:

$$Q_n^c = \mu\ T_n = E_n\mu\ \left(1-\exp\left(-k\,LAI_n\right)\right) \tag{11}$$

where μ is the Water Use Efficiency.

From the individual plant production equation of GreenLab (3) and in the case of a homogeneous crop of density d, the biomass production per unit surface area is directly deduced:

$$Q^c{}_n = E_n\,\beta\,d\ \left(1-\exp\left(-\eta S_n\right)\right) \tag{12}$$

Let $S_d=1/d$. For a homogeneous crop, $LAI_n = S_n/S_d$, by identifying (11) and (12), the empirical parameters β and η are thus given by $\beta=\mu S_d$ and $\eta=\mu/S_d$. This analogy helps us derive a general formulation for the individual plant production equation:

$$Q(n) = E(n)\,\mu\,S_p\left(1-\exp\left(-k\,S(n)/S_p\right)\right) \tag{13}$$

S_p is a reference surface, such that $S_p=S_d$ in the case of homogeneous high density crops (see the application to maize for different densities in Ma et al 2008). In the case of spatially heterogeneous crops (like rapeseed fields), a Voronoi tessellation can help determine the S_p of all individuals in the population. For tree communities, things can get far more complex. First, the reference surface

can not be taken as a constant: it increases along plant growth. Cournède et al. (2008) proposed to model it as a function of the leaf surface: $S_p(n)=S_p^0(S_n/S_p^0)^r$. Simulation results are shown in Fig. 7, which shows the impact of density on tree architecture. It was tested successfully by Letort et al. on beech tree (2008, submitted). Moreover, a generalized Poisson model of leaf repartition inside the canopy was proposed by Cournède and de Reffye (2007) to compute plant production for individuals in heterogeneous and potentially multi-specific tree stands. Although the simulation results are encouraging, this model still lacks field validation.

5 Conclusion and Discussion

The GreenLab model catches the main growth processes, by integrating the competition and production of biomass. The model is proved to be generic to simulate plants of various architectural models. When difference is discovered between the behaviour of model and experimental data, it reveals lack of information in the model: some important ecophysiological process might not be taken into account, and further experimental studies are required. Theoretical work can push experiment and experiment provides knowledge to model. In a spiral way, through interaction between model and experiment, knowledge on plant can be increased. GreenLab provide such a tool that integrates knowledge, and help improving understanding of the complex plant system.

The mathematical formulation of GreenLab allows a theoretical study of model behaviour, prior to application to real plants. At beginning the main interest was the calibration of model for a plant under fixed environment. With the achievement on theoretical computation, such as plant optimization, possible link with QTL and plant competition, new focus will be on the genetic difference, and cultivation strategy. Actually such work has begun already.

In GreenLab, there are still several empirical parameters that lack explicit physical meanings. With more and more application, the next step may be link the parameters with actual measurable values, so that it is easier to compare the parameters of plants under different condition, or even compare the parameters for different species. A link between GreenLab and traditional physiological models may benefit to each other.

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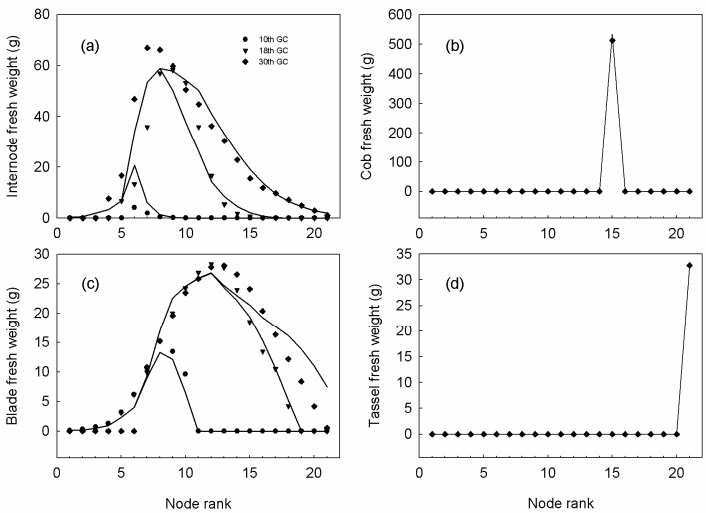
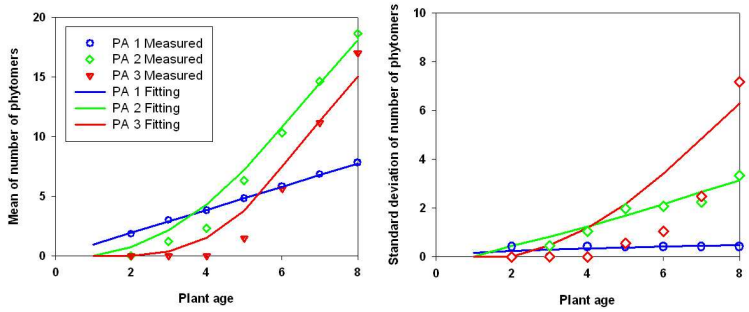
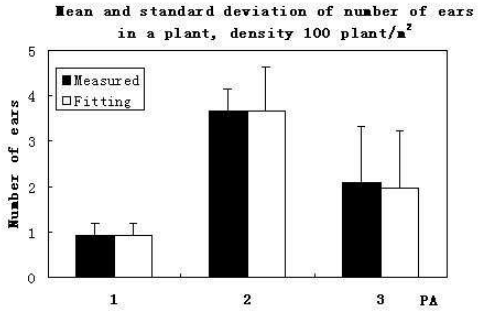


Fig. 1. Fitting GL1 to maize plants using measured data at three ages (i.e., 10, 18, and 30 GC, respectively) simultaneously. Target data are organ fresh weights (a) for internode, (b) for the cob, (c) for leaf blade, and (d)

for the tassel. (Leaf sheath weights are also fitted, data not shown.)

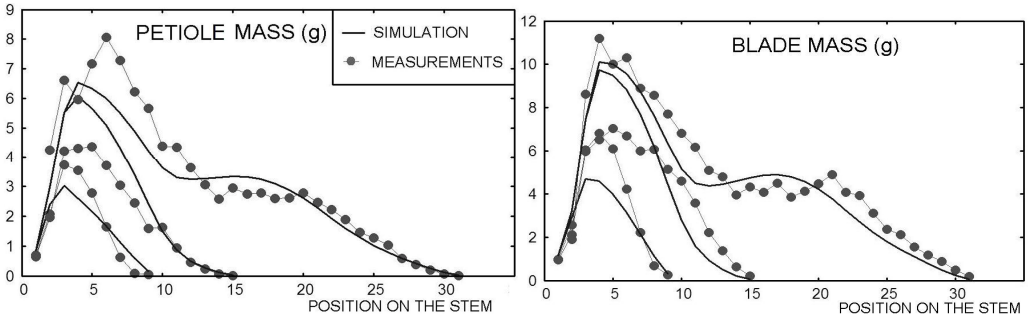


(a) (b)

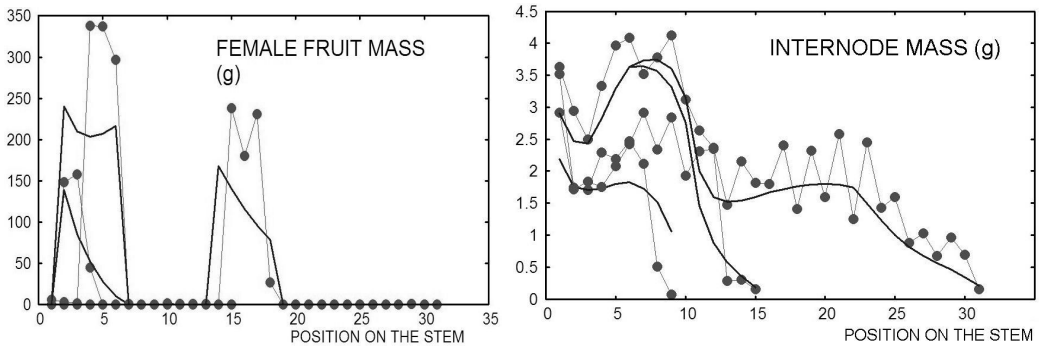


(c)

Fig.2. The mean and standard deviation of the number of phytomers and ears in main stem (PA 1), primary tillers (PA 2), secondary tillers (PA 3) of a wheat plant, with population density 100 plants m^{-2}, fitted with GreenLab organogenesis model (lines).

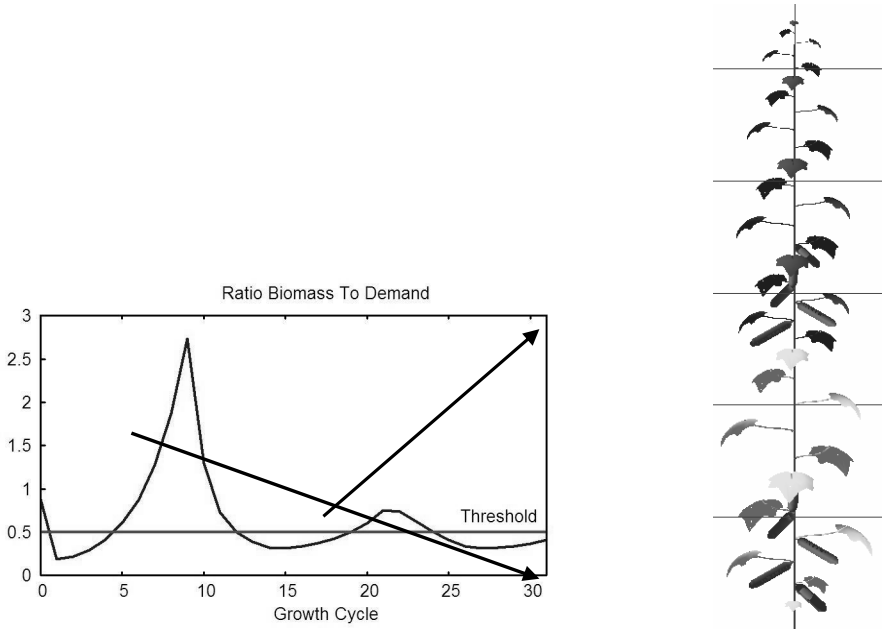


(a) (b)



(c) (d)

Fig. 3. Simulation and measurement for a cucumber plant at three different ages (9GC, 15 GC, 31 GC). We used a multifitting procedure with the same set of source-sink parameters. The variations in the phytomer profile along the stem are a consequence of the competition between sinks.



(a) (b)

Fig. 4. Ratio of biomass production to demand as a function of growth cycles and corresponding plant. Horizontal line represents threshold value (a). When the ratio exceeds this value, fruits grow on the main stem. Two timeframes in which fruit set can take place are observed (b).

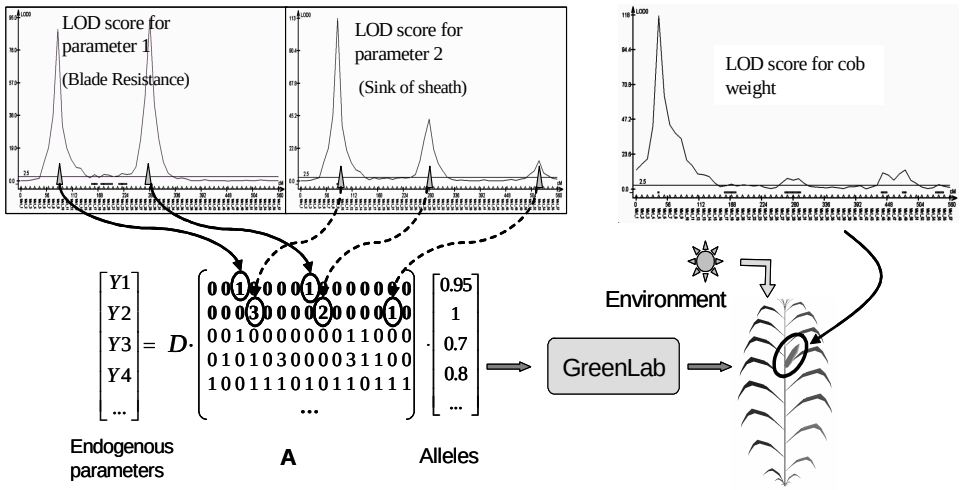
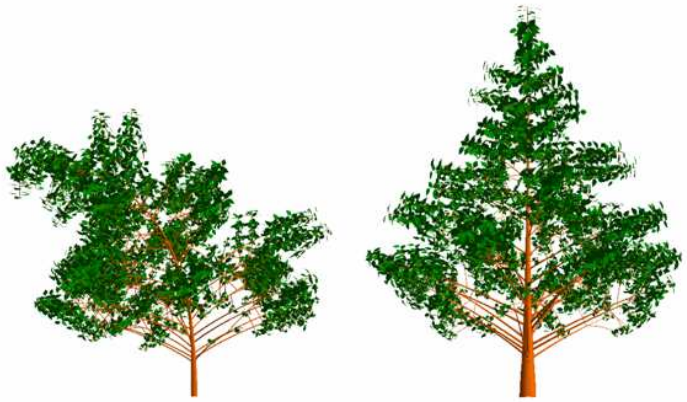


Fig. 5. Simulation of QTL detection: GreenLab parameters (*Y*) are determined through a simple genetic model (matrix multiplication *D*, *A*) from the allele values. The graphs represent the results of QTL detection using a virtual mapping population when traits are model parameter compared to the case where the trait is cob weight.



(a) (b)

Fig. 6. 3D illustration of wood quality and quantity, for a 40 years old virtual tree. (a) trunk weight 5.04E+4g (b) trunk weight 2.45E+5g.

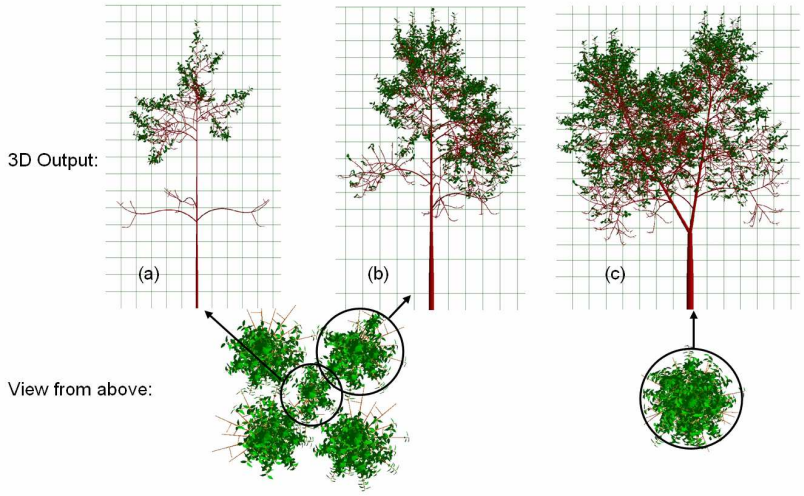


Fig. 7: Simulation and visualization of trees (of the same species) growing in different conditions of competition: in a clump for individuals (a) and (b) and in open-field conditions for (c).